POLSKIE PISMO ENTOMOLOGICZNE
BULLETIN ENTOMOLOGIQUE DE POLOGNE
Tom 64: 279-294 Wrocław 30 XII 1995

4TH SEMINAR ON APTERYGOTA, BIAŁOWIEŻA, POLAND, 1994

The biogeography of *Collembola*

KENNETH CHRISTIANSEN[1], PETER BELLINGER[2]

[1] Grinnell College, Grinnell, IA 50112, USA
[2] California State University, Northridge, CA 91330, USA

ABSTRACT. The authors review the present status of our knowledge concerning the biogeography of *Collembola*. They present some ideas arising from the views concerning regional relationships as presented by recent authors. They also look at recent analyses of biogeographic relationships of specific taxonomic groups. They use JACCARD'S number to furnish a quantitaive analysis of the biogeographical relationships among *Collembola*. The major conclusion is that relatively recent tectonic events and movements are largely responsible for patterns of *Collembola* distribution.

INTRODUCTION

CASSAGNAU (1990) in an excellent brief introduction to *Collembola* biogeography, points out that the nature of *Collembola* with their limited mobility and frequent stenotypy makes them excellent animals for biogeographic study. We recommend this as a good introduction to this area of study.

MICROGEOGRAPHIC VARIATION

A number of authors have analyzed in detail the microgeographic variation of one or a few species. CHRISTIANSEN, CULVER (1968, 1969) studied microgeographic variation and evolution in two widespread species of cave *Collembola* and three troglobtic cave species of

Pseudosinella from Pyrenees caves were studied by CHRISTIANSEN and BOUILLON (1978). I (CHRISTIANSEN 1958) examined the morphological variation in *Entomobrya* (*Entomobryoides*) *guthriei*.

The discovery of giant salivary gland chromosomes in *Neanurini* has made a series of analyses of caryotypic variation possible. CASSAGNAU (1975) CASSAGNAU et al. (1979) and DALLAI (1979) DEHARVENG (1984), DALLAI (1979).

Overall there does not appear to be any clinal or geographically patterned distribution of caryotypes. The authors suggest the possibility that the caryotypes are more closely related to ecological conditions or adaptive functions than evolutionary pattern.

More recently modern techniques have been used to study the genetic sturcture of *Collembola* populations (FANCIULLI et al. 1986[b]). In the polytene species so far studied there is no good agreement between caryotypic difference and genetic distance (DALLAI et al. 1983, FANCIULLI et al. 1986 and 1986[a]).

Other informative studies have been made (FRATI, FANCIULLI, DALLAI 1992, FANCIULLI et al. 1991, FANCIULLI et al. 1986, FRATI, FANCIULLI, POSTHUMA 1992).

Overall the one striking conclusion from these studies is that there is no universal or even general pattern visible in microgeographic variation in *Collembola*. To the contrary the type of pattern varies from region to region, group to group and even species to species. Each microgeographic pattern seems to be responding to a different set of controlling factors and produces a quite unpredictable and chaotic result.

SUPRASPECIFIC TAXON ANALYSES

A number of authors (THIBAUD 1990, VASQUEZ, PALACIOS-VARGAS 1989, DALLAI, FANCIULLI 1985, POINSOT, DALLAI 1971, CASSAGNAU, DEHARVENG 1980, MASSOUD 1967, DALLAI 1983, CASSAGNAU 1983, GREENSLADE, DEHARVENG 1991) have analyzed the distribution of particular supra-specific taxa it is possible to explain most of these distributions on the basis of plate tectonic events of different times and many of the authors offer just such explanations. Caution should be used in using studies before 1990 as many of the conclusions from these studies must be altered in the light of later discoveries which either fragment genera or show that some recent genera are polyphyletic and thus invalid for evolutionary analysis.

Ecological rather than geographic factors appear to be most important in the detailed analysis of seven species of European

Sminthurids described by BRETFELD (1989). MURPHY'S study (1971) of *Pseudanurida* is quite different and shows a wide distribution and represents the special case seen in marine littoral forms.

HABITAT TYPES

Littoral *Collembola* have been studied by a number of researchers (STRENZKE 1955, WITTEVEEN 1986, SCHUSTER 1962, 1963, THIBAUD, NAJT 1993), GREENSLADE 1983, CHRISTIANSEN, BELLINGER 1988, CHRISTIAN 1989) A common pattern is for closely related species to have disparate ranges. A second pattern is for widely disparate collections. A third pattern is for one widespread species to occur without close evolutionary connections to any other littoral species. Given the ease with which the thalasobiont species should be transported, the extreme localization of many species is difficult to explain. The simplest explanation is inadequate collections; however, the difference in range seen in some related species makes this explanation questionable. It is possible that random rare colonization or special ecological requirements afford the correct explanation.

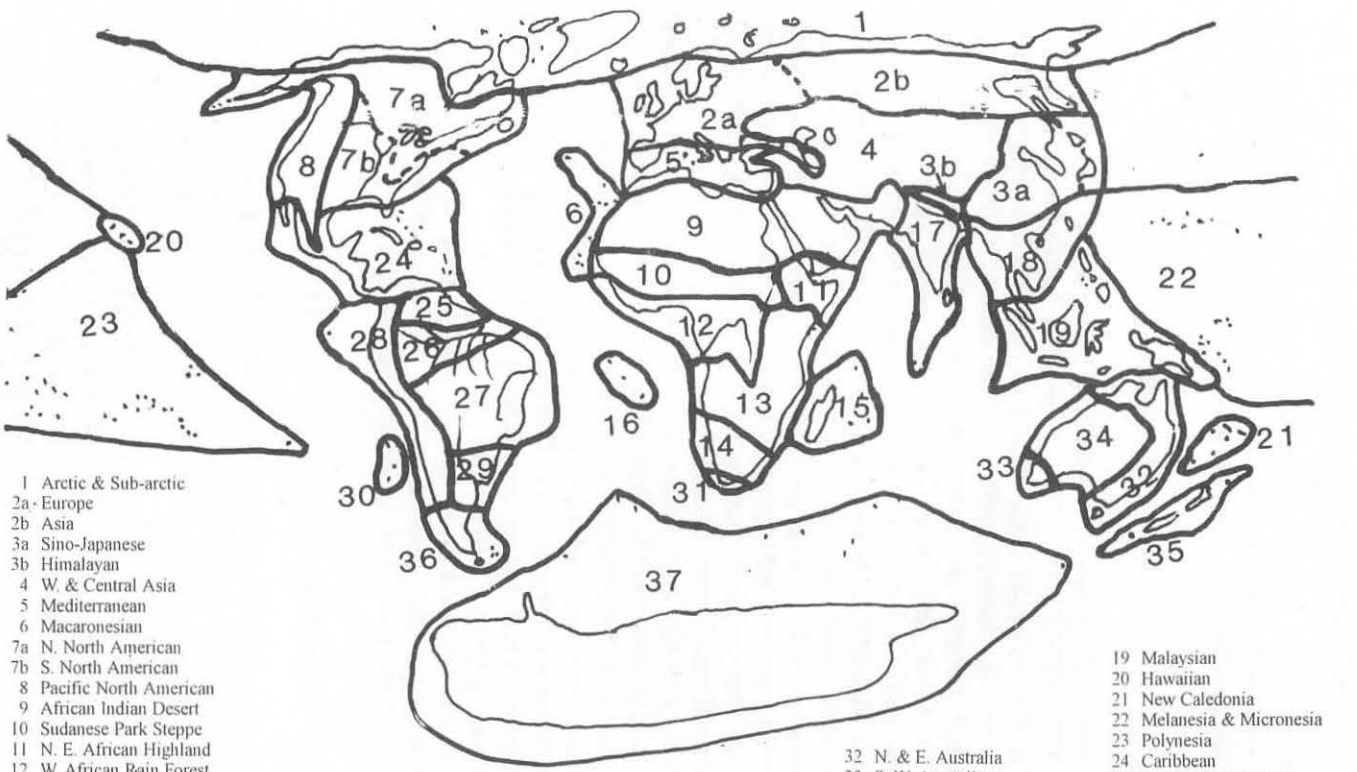
At the other extreme cave *Collembola* should have the least capacity for transportation and should thus offer excellent vehicles for biogeographic analysis. CHRISTIANSEN (1982), STOMP (1986) and DAGAMA (1991) showed that troglophile species generally have much wider distributions than troglobiont ones. CHRISTIANSEN and CULVER showed that both dispersionist and vicariant events were important in explaining the distribution of cave *Collembola*.

BLACKITH (1981) looked at tundra *Collembola* using principal coordinates analysis. He showed a close relationship on a basis of geographic proximity but not on ecological factors.

GLOBAL INTERRELATIONSHIPS

BLACKITH and BLACKITH in 1975 examined the factors limiting *Collembola* distribution using 70 species lists and principal coordinates analysis. Unfortunately some of the lists used were totally unreliable and thus distorted the results.

We used a modified version of GOOD'S (1974) plant biogeographic provinces to study the global distribution of about 6,200 species of *Collembola*. We modified the system by lumping the south temperature oceanic Islands with Antarctica and dividing his Sino-Japanese region (3) into Sino-Japanese (3a) and the Himalayan region (3b). (Fig. 1). These data are not given in this paper but are available on computer



1 Arctic & Sub-arctic
2a Europe
2b Asia
3a Sino-Japanese
3b Himalayan
4 W. & Central Asia
5 Mediterranean
6 Macaronesian
7a N. North American
7b S. North American
8 Pacific North American
9 African Indian Desert
10 Sudanese Park Steppe
11 N. E. African Highland
12 W. African Rain Forest
13 E. African Steppe
14 South African
15 Madagascar
16 Ascension & St. Helena
17 Indian
18 Continental S. E. Asia
19 Malaysian
20 Hawaiian
21 New Caledonia
22 Melanesia & Micronesia
23 Polynesia
24 Caribbean
25 Venezuela & Guiana
26 Amazon
27 South Brazilian
28 Andean
27 Pampas
30 Juan Fernandez
31 Cape
32 N. & E. Australia
33 S. W. Australia
34 Central Australia
35 New Zealand
36 Patagonian
37 Antarctic & Subantarctic

1. Modified GOOD (1974) biogeographic provinces

disk upon request from one of the authors. The distributions were first examined in 4 family clusters and then lumped together. We examined both the numbers of shared species and JACCARD'S index. JACCARD'S index is the more meaningful measure of relatedness as it adjusts for bias as a result of large numbers of species recorded. As HENGVELD (1990) has pointed out this measure of biogeographic relationship gives the fewest problems and its results are easiest to interpret. This measure is achieved by: N. shared species / N. shared species + N species found in one or other region but not shared. High (.20 or higher) JACCARD'S numbers are found among the 3 North American regions (7a, 7b, and 8), the Arctic and northern N.A. (1 & 7a), Western Europe and the Mediterranean region (2a & 5) and the 3 Australian regions (32-33 & 34). These relatively close relationships are found in all the family groups except for a relatively weak connection in the Australian region in the *Hypogastruridae* s.l.

The Arctic and Subarctic regions (1) shows an overall moderately strong relationship (.19-.20) to Asia and Northern Atlantic North America, and a moderate relationship (.11-.14) to the rest of the North American cluster (7b & 8), west and Central Asia (4), Europe (2a) and the Mediterranean (5). The Macaronesian region (6) shows its strongest relationship (.17) to the Mediterranean region (5). These relationships vary greatly in the different family groups.

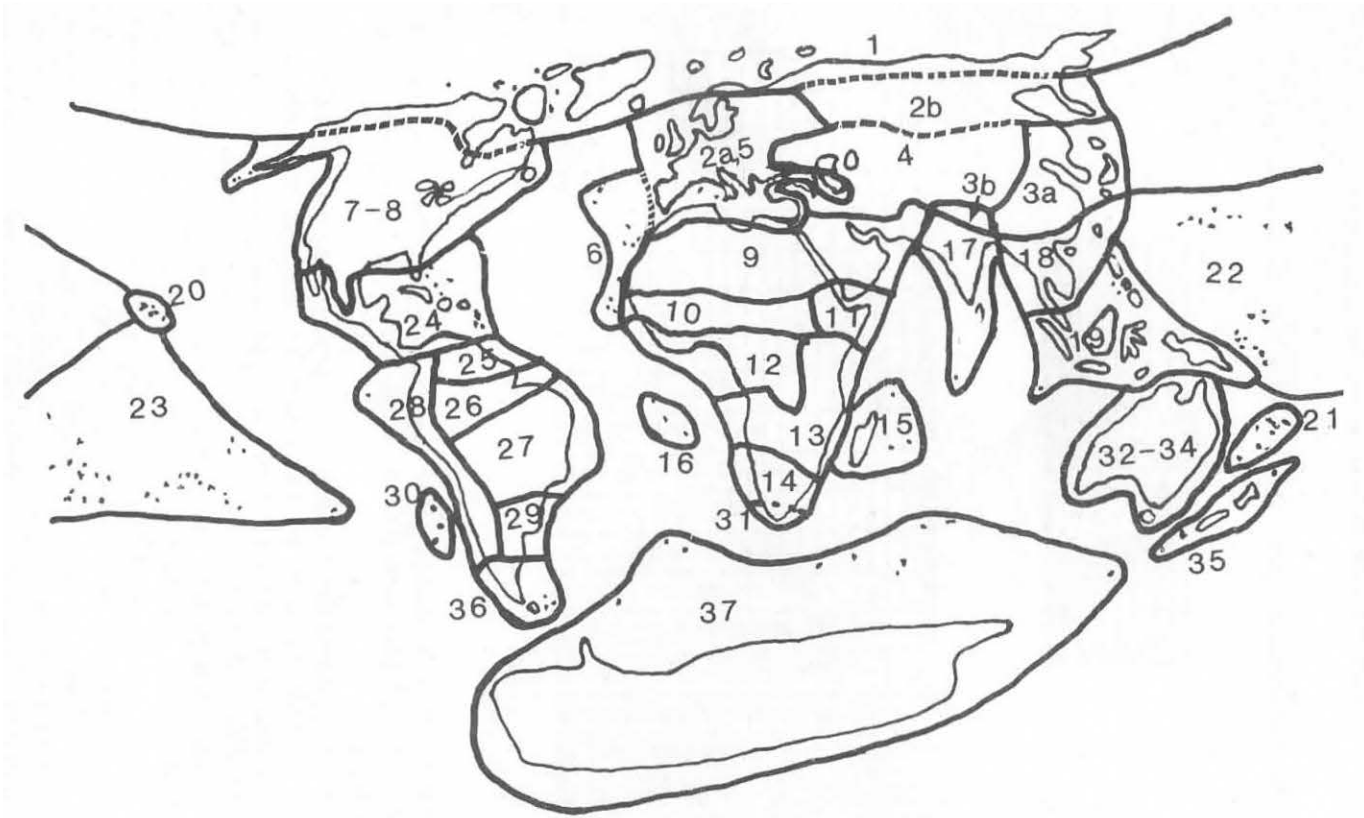
When considering all of our modified GOOD regions, those with very small numbers of species (fewer than 75) generally show no clear similarity (all overall JACCARD numbers below .06). One exception is South Africa (14) which has clear relationship (.15) to Cape province (31) and a slight one (.07) to East African Steppe (13). Almost all of the regions with more than 75 species show at least a slight resemblance (JACCORD'S between .06 & .10) to some regions. The four rather surprising exceptions to this are west African Rain Forest (12) with 173 species, the Antarctic-Subantarctic (37) which has 127 species and the Himalayan region with 193 species and no clear overall relationships above .06. The Sino-Japanese region with 551 species (3a) and only one overall relationship above .06 and that .07. The S. Asia cluster (17, 18, & 19) show weak relationships only to each other except for 19 which also shows a weak relationship (.07) to Melanesia (22). The North American cluster all show a slight additional weak (.07-.09) relationship to the Mediterranean, Macaronesia, Hawaii and the Caribbean (5, 6, 20, & 24). Most of the remaining weak relationships are clearly the result of proximity. Thus New Zealand (35) is only related to all 3 Australian regions but surprisingly not to the Antarctic cluster (.04). The number of species the Antarctic cluster

shares with New Zealand is surpassed only by that with Australia and Europe and the low JACCARD's number is probably brought about by the large number of New Zealand endemics.

When family groups are examined proximity again appears to be the primary factor influencing similarity among continental regions. The arctic Subarctic shows clear relationships only to the neighboring North American and Asia regions (7A, 8, & 2b) except in the neelid-sminthurid group where it shows a connection to regions 4-6. The East and South African regions (13 & 14) mainly show continental region relationships to each other and 9. Slight relationship (.11) is shown in the West African region (12) only to the Sudanese Park Steppe (10), in the Hypogastruridae s.l. and Ascension Island (16) has only one significant relationship, with the Sudanese (10) Park Steppe. in the *Onychiuridae-Isotomidae* group.

Overall the results clearly show that proximity is the strongest factor influencing continental species similarity. This suggests that species similarity results from relatively recent interactions. They also seem to require some modification of the GOOD system (Fig. 2) as shown here. Regions 2A & 5 are lumped as are 7A B & 8 and all 3 Australian regions. In addition the similarity between region 1 and North America and Northern Asia, between 2b and 4, as well as that between Macaronesia and the Mediterranean zone shows that these regions are closely linked while 31 (Capetown) is equally closely linked to South Africa (shown by the broken lines separating all these areas). In contrast the relatively weak connection between 2A & 2B (as contrasted to that between 2b & 1 or 4 or even 2a & 1) requires a sharper separation between these areas. This break suggests that the Ural Mts. have been a more effective barrier between the two regions than other mountain ranges such as the Rocky Mts. in N. America and the Andes Mts. in S. America.

When the fused units' JACCARD numbers are examined the basic situation remains unchanged from that described above (see Table 1). Here we have eliminated regions where there is no JACCARD value above .05. In this we see the closest relations of 7-8 (NA) are with the Arctic (.15) and Caribbean (.09). The Australian region (32-34 = AU) is now closest to Macaronesia and New Zealand (.08). All these results point to the Collembolan fauna of the Holarctic region being very tightly linked and divided into two large blocks. The first includes North America, the Arctic and Subarctic regions, Asia and W. & Central Asia. The second includes Europe, the Mediterranean and Macaronesia. The position of the Sino- Japanese region is problematic but clearly its closest relationship is with the first region rather than



2. New suggested biogeographic provinces

Table 1
JACCARD number for groups where number is > .05 for some member

Jaccard number regions.
EU = 2a+5, NA=7+8, Au= 32-34

Holarctic Cluster

1	**.11**	.04	X					
EU.	**.07**	.03	**.09**	X				
2b	**.11**	.04	**.19**	**.06**	X			
3a	.05	.04	**.06**	.03	**.06**	X		
4	**.09**	.04	**.11**	**.06**	**.16**	.04	X	.
NA	**.06**	**.09**	**.15**	**.06**	**.06**	**.06**	.05	X
	6	24	1	EU	2b	3a	4	NA
N. spp	186	77	339	1852	231	551	324	1002

Remaining Continental Region's with at least one Jaccard number> .05

9	X																	
13	.02	X																
14	.05	**.07**	X					numbers above .05 in **bold face**										
17	.02	.03	.03	X														
18	.02	.01	.01	**.07**	X													
19	.05	.01	.01	.05	**.07**	X												
22	.03	.01	.01	.02	.04	**.07**	X											
23	.03	.02	.02	.03	.03	.02	.05	X										
24	.04	.01	.02	.03	.02	.03	.02	.01	X									
26	**.07**	.02	.02	.03	.03	.02	.03	.01	**.06**	X								
27	.03	.03	.03	.03	.01	.02	.02	**.06**	.05	**.09**	X							
28	.05	.02	.03	.03	.03	.02	.03	.03	**.06**	**.09**	**.06**	X						
29	.04	.02	.03	.04	.02	.02	.02	.03	.05	**.07**	.04	**.14**	X					
30	.03	.01	.05	.01	.01	.01	.02	.02	.01	.04	.01	.04	.03	X				
31	**.06**	**.08**	**.15**	.04	.01	.02	.01	.04	.03	.04	.04	.05	**.06**	**.06**	X			
AU	.03	.02	.02	.04	.03	.03	.05	.03	.04	.02	.03	**.06**	**.06**	.02	**.06**	X		
35	.02	.01	.02	.02	.01	.01	.02	.02	.02	.02	.02	.03	.04	.02	.04	**.08**	X	
36	.00	.00	.00	.01	.01	.01	.01	.01	.01	.02	.01	.05	**.06**	.04	.02	.02	.01	X
37	.01	.00	.02	.01	.01	.01	.01	.00	.02	.01	.02	.03	.04	.03	.03	.05	.04	**.06**	X
	9	13	14	17	18	19	22	23	24	26	27	28	29	30	31	AU	35	36	37
N. spp	68	143	47	264	273	337	77	35	437	94	100	157	234	15	78	355	287	64	121

Continental S.E. Asia or any other region. Similarly the 2a, 5, 6 region is clearly more closely linked to the other Holarctic block than to any other region.

In order to examine the possibility that generic distributions reflected old plate tectonic patterns we examined the JACCARD'S numbers of generic distributions. We eliminated from consideration form genera such as *Sinella* and *Pseudosinella* which are obviously polyphyletic. We also eliminated genera which occur in only one GOOD region as being uniformative. We then treated the presence or absence of any member of the genus in a region in the same fashion as we had treated the presence or absence of a species. We also considered three different situations: 1) where any species of the genus occurred in the region, 2) where 2 or more species occurred and 3) where 5 or more species occurred. The second of these measures is probably the best measure of generic similarity because it eliminates or diminshes the

effect of "global" species. It is very probable that many of these are tramp species and others are taxonomic fictions (*Ceratophysella denticulata* ex.) as a result of our poor taxonomic knowledge. In both cases they are uninformative or misleading. At the other extreme the 5 shared species severely limits the actual data available.

In all the results the most important single factor in determining generic similarity seemed to be proximity. For example when all GOOD regions were considered, and Island areas or those with fewer than 50 species were eliminated, 30% of all large values (over .30) were between contiguous regions, and many of the remainder were separated by just one region. There was little evidence to support a primary role for Gondwanaland connections. For example, the closest generic relationships of India are with Continental S.E. Asia and Malaysia. There is a greater generic similarity between India and various other regions in the different studies than between India and any area of old Gondwanaland. Similarly Madagascar, in what is probably the most reliable measure of generic relationship (2 or more species shared), is most similar to the 3 neighboring African regions and is more similar to S.E. Asia than to India and shows no strong similarity to other Gondwanland regions. African and South American regions generally show little generic affinity to other Gondwanaland areas. The one exception to this is a relatively strong relationship between Australia and the Pampas region. A hint of old Gondwanaland connection is given by the fact that interrelationships among these regions tends to be stronger in the measure of 5 or more shared species than in the other two levels. All of this requires reexamination of the various Godwanaland distributions used to explain many *Collembola* present day patterns.

The old Laurasia group shows strong interrelationships but these are not strikingly different from those seen in the species relationships. Thus the conclusion we draw is that generic as well as species distributions of continental groups have largely been shaped by relatively recent events. This is not to say that specific genera may not reflect very old tectonic patterns but just that overall this does not seem to be the case.

REGIONAL ANALYSES

Many authors have examined the biogeographic relationships of different regions. These studies can be divided into two large categories - continental and island studies. The great majority of these analyses have been done on Eurasian and North African regions with emphasis on mountain systems (AGRELL 1943, NOSEK 1969, DUNGER 1969, 1970,

1975, 1985, WEINER 1977, 1981, SZEPTYCKI 1967, THIBAUD, MASSOUND 1980, POINSOT 1974, DALLAI 1970, 1971). A serious problem in any quantitative comparison among these different works is the fact that they rarely if ever use comparable biogeographic subdivisions. In the 10 works of this sort which we examined no term was used in all studies. The widespread category was most frequent but this was very differently defined. In some it included only "cosmopolitan" species; in others it included Palearctic, Holarctic, central European or more widespread forms. Endemic species was a common category but this was sometimes merely by default. That is, some species were described as new in the works and thus became endemic by default with no other endemic species indicated.

RAPOPORT analyzed the *Collembola* of the New World tropics in a pair of papers (1968 & 1971). He subdivides the New world tropics in a fashion somewhat similar to that of GOOD. He also examined the fauna of Antarctica and the periantarctic islands. He also in his table 6 shows the numbers of species shared among these regions and gives the coefficient of similarity for the Latin American forms. Many of his fugures (viz. those involving North America and the Antilles), are very different from those seen in our studies as a result of newer discoveries.

However, many of the conclusions to be drawn from his study are probably still valid. First it is notable that the widespread or cosmopolitan group is very abundant in all regions except Antarctica and the Antilles, ranking 2nd or 3rd in all cases. A surprisingly high relationship to the Palearctic region (ranking generally 4th or 5th) may be accounted for by a large number of introduced species. Within the new world the closest correlation between factors and fauna appears to be geographic separation rather than ecological similarity. Thus the Andean-Patagonian region which should probably be ecologically most similar to the Araucanian region is far more similar to the Guyano-Brazilian (coefficient of similarity 16.2 compared to 9.49).

GREENSLADE in a series of articles (DA GAMA, GREENSLADE 1981, GREENSLADE 1982, 1987) examined Australian collembolan biogeography. She notes a strong Asiatic connection which probably represents a later invasion and is more prominent in arid regions than the older Gondwanaland connections.

THIBAUD (1991) summarized the biogeographic conclusions deriving from a series of papers he and MASSOUD had published between 1979 and 1987 concerning the Lesser Antilles. We expanded this consideration to include the Greater Antilles We used JACCARD's measure as an indication of faunal similarity. Unsurprisingly the closest relationship

of the two groups of Islands were with each other. Several interesting things can be observed. First, proximity cannot be the primary explanation for faunal similarity. The closest island of the Greater Antilles (Puerto Rico) is the least similar to the Lesser Antilles. Similarly, while Jamaica is much closer to Cuba than Puerto Rico they have identical similarity indices.

There have been a number of studies of Mediterranean Islands concerning biogeography (DALLAI 1973, 1976, 1983, DEHARVENG 1980, PARISI 1969). All are agreed that the present day distribution probably reflect plate tectonic separations from the mainland and, in archipelagos, possibly from each other.

The biogeography of the subantarctic islands has been examined a number of times (DEHARVENG 1979, RAPOPORT 1971, TRAVE 1987, GREENSLADE 1990). The strongest relationships are with Antarctica, the Patagonian and Australian regions and other subantarctic islands. A weaker link is seen with Cape province. All clearly belong to the group called "cold Gondwana" by CASSAGNAU (1990). The great similarity between the endemic species and those from other regions argues for a relatively recent introduction of these groups.

The Hawaiian archipelago is a unique case. First it has never been connected to continents and second this is the most isolated archipelago. We studied the biogeography of the *Collembola* of these islands in detail (CHRISTIANSEN, BELLINGER 1994). Endemicity appears to be related to age of the region, to habitat type, and perhaps to altitude. The Hawaiian fauna appears to have been recruited primarily from North America and the Sino-Japanese region, with tropical southeast Asia providing a smaller component. Modes of immigration are uncertain, but ocean transport seems most likely for endemics of North American and oriental origin, especially mobile members of the *Entomobryidae* and *Sminthuridae*; bird and/or wind transport may also have played a role.

Much of the original native fauna has probably become extinct; the rate of extinction has been declining this century, and the remaining endemic species are mostly generalists which are relatively tolerant of altered conditions; the same is probably true of successfully introduced exemic species, whose rate of extinction has been low. Most exemic species were probably introduced before the middle of the century, and perhaps much earlier. Thus we can expect little change in the *Collembola* fauna in the near future. There appears to be a low rate of speciation of *Collembola* in Hawaii in comparison to insects or even flowering plants.

CONCLUSIONS

Our first and strongest conclusion is that while many excellent studies have been done on biogeography of *Collembola* these have suffered greatly from a lack of uniformity of biogeographic provinces or subdivisions. We urge that large scale subdivisions follow the modified Good divisions which we have adopted as shown in Fig. 2. We suggest the Term North American (N.A. for fused regions 7a 7b & 8. The term Australian for fused regions 32-34 and Euro-Mediterranean for fused regions 2a & 5. We also suggest the name Old Holarctic for fused regions 1-2b-4-7-8. We suggest the term Greater European for regions 2a, 5 & 6. The European region also need to be divided into general provinces but we do not presume to do this here. We suggest some European researcher engage in this task.

We also conclude that most present day *Collembola* distributions have been determined by relatively recent geological events and that most ancient plate tectonic events have been overwhelmed by more recent distribution patterns. We have not attempted to match our patterns with recent geological events; however we suspect that most would have resulted from tertiary or later events. One could certainly use our computer data to analyze this question.

Our last conclusion is that while micro geographic studies have been interesting and often exciting there is a need to integrate these and use past works to deal with problems in a new fashion now that the tools of genetic analysis are widely available. For example a genetic analysis of our detailed studies of morphological and behavioral variation in cave *Pseudosinella* could afford great insights into the nature of evolutionary processesand biogeographic movement.

ACKNOWLEDGMENTS

We would like to thank EMILY MOORE who performed the JACCARD analyses for us and THOMAS MOORE who assisted in the mathematical work, ROY RICH entered the data into our computer system for us. GLENN LEGGETT assisted us in the editing of the manuscript. This work was made possible by a research grant from Grinnell College.

REFERENCES

AGRELL, I., 1943, Kritiches Verzeichnis der Schwedischen Collembolen mit einige Neube-schreibungen und tiergeographischen Erörterungen. Opuscula Entomologica. **8**: 123-137.

BELLINGER, P., K. CHRISTIANSEN, 1990, Biogeography of the *Collembola* of Hawaii. (In:) R. DALLAI (ed.), 3rd International Seminar on *Apterygota*, University of Siena: 121-126.

BLACKITH, R. E., 1981, The *Collembola* of the tundra biome sites: a zoogeographical synthesis, (In:) BLISS, L.C. et al. (eds), Tundra Ecosystems: a comparative analysis: 541-545. Cambridge univ. Press.

BLACKITH, R. E., R. M. BLACKITH, 1975, Zoogeographical and Ecological Determinants of Collembolan Distribution, Proc. Royal Irish Acad. **75B**: 345-368.

BRETFELD, G., 1989, Chorologie und Ökologie von sieben europäischen Arten der *Collembola-Sympholpleona* (*Insecta, Entognatha*), Zool. Jb. Syst. **116**: 293-327.

CASSAGNAU, P., 1975, Le polymophisme des Chromosmes polytenes de *Bilobella aurantica* CAROLI (collemboles) et sa signification biogéographique et écologique, C. R. Acad. Sci. Paris **280**: 2777-2780.

CASSAGNAU, P., 1979, Les Collemboles *Neanuridae* des pays Dinaro-balkanique: leur intéret phylogénétique et biogéographique, Biologia Gallo-Hellenica **8**: 185-203.

CASSAGNAU, P., 1983, Introduction a l'letude phylogénétique et biogéographique des Collemboles *Neanururidae*, Pedobiologia **25**: 293-299.

CASSAGNAU, P., 1990, Des hexapodes vieux de 400 millions d'années: les Collemboles. 2. Biogeographie et écologie, Anné Biol. **29** (1): 1-69.

CASSAGNAU, P., 1991, Biogeographie des Collemboles *Neanurinae* des Montagnes du sud de l'Inde et de Sri Lanka. (In:) VEEREESH G.K., D. RAJAGAPOL (eds), Advances in Management and Conservation of Soil Fauna: 39-45.

CASSAGNAU, P., R. DALLAI, L. DEHARVENG, 1979, Le polymorphisme des chromnosomes polytenes de *Lathriopygia longiseta* CAROLI (Collembole *Neanuridae*), Caryologia **32**: 461-483.

CASSAGNAU, P., L. DEHARVENG, 1980, Sur l'interet Biogéographique et cytonegéntique d'un nouveau genre de Collemboles *Neanuridae*: *Travura* n.g., Trav. du Lab. d'écobiologie des Arthropodes Edaphiques **2**: 1-11.

CHRISTIAN, E., 1989, Biogeography, substrate preference, and feeding types of North Adriatic intertidal *Collembola*, Marine Ecology **10**: 79-94.

CHRISTIAN, E., C. KAMPICHLER, 1984, Zur zoogeographie einiger epedaphischen Collembolen aus östlichen niedorösterreich, Ann Naturhist. Mus. Wien **86**: 133-139.

CHRISTIANSEN, K., 1956, The genus *Mesentotoma* (*Collembola, Entomobryidae*), Psyche **63**: 14-20.

CHRISTIANSEN, K., 1958, Geographic variation and the subspecies concept in the collembolan *Entomobryoides guthriei*, Syst. Zool. 7: 10-15.

CHRISTIANSEN, K., 1971, Notès on Miocene amber *Collembola* from Chiapas, Univ. Calif. Publ. Entomol. **63**: 45-48.

CHRISTIANSEN, K., 1982, Zoogeography of cave *Collembola* east of the great plains, N.S.S. Bull. **44**: 32-41.

CHRISTIANSEN, K., P. BELLINGER, 1988, Marine littoral *Collembola* of North and Central America, Bull. Marine Sci. **42**: 215-245.

CHRISTIANSEN, K., P. BELLINGER, 1994, The Biogeography of Hawaian *Collembola*: the simple principles and complex reality, Oriental Insects **28**: 309-351.

CHRISTIANSEN, K., M. BOUILLON, 1978, An Evolutionary and Ecological Analysis of the terrestrial arthropods of caves in the central Pyrenees, N.S.S. Bull. **40**: 114-117.

CHRISTIANSEN, K., D. CULVER, 1968, Geographical variation and evolution in *Pseudosinella hirsuta*, Evolution **22**: 237-255.

CHRISTIANSEN, K., D. CULVER, 1969, Geographical variation and evolution in *Pseudosinella violenta*, Evolution **23**: 602-621.

CHRISTIANSEN, K., D. CULVER, 1987, Biogeography and distribution of cave *Collembola*, Jour. Biogeogr. **14**: 459-477.

CRISCI, J. V., CIGLIANO, J. MORONE, S. ROI-JUQEZ, 1991, Historical biogeography of Southern S. America, Systematic Zool. **40**: 152-171.

CULVER, D., 1970, Analysis of simple cave communities. I. Caves as islands, Evolution **24**: 463-474.

DALLAI, R., 1970, Ricerche sui Collemboli. XIV. Le alpi Apuane, Lavori della Soc. Ital. Biogeografia (2) **1**: 433-482.

DALLAI, R., 1971, Ricerche sui Collemboli. XV. I Monti Reatini ed alcuni rilievi abruzzesi, Lavori della Soc. Ital. Biogeografia (2) **2**: 323-378.

DALLAI, R., 1973, Ricerche sui Collemboli. XVII. Le isole Eolie. Lavori della Soc. Ital. Biogeografia (2) **3**: 481-590.

DALLAI, R., 1976, Ricerche sui Collemboli. XXII. Le piccole isole dell'arcipelago toscano, Lavori della Soc. Ital. Biogeografia (2) **5**: 509-521.

DALLAI, R., 1979, Polytene chromosomes of some *Bilobella aurantica* (*Collembola*) Italian populations, Boll. Zol. **46**: 231-249.

DALLAI, R., 1963, Interesse biogeografico dei Neanuridi (*Collembola*) della Sardegna e delle isole dell'Arcipelago Toscano, Lavori delle Societa Ital. di Biogeografia (2) **8**: 417-465.

DALLAI, R., P. P. FANCIULLI, 1982, I cromosomi politenci di alcune poplazioni di *Lathriopygia longistea* (*Insecta*, *Collembola*) della Toscana Meridionale, Redia **65**: 9-28.

DALLAI, R., P. P. FANCIULLI, 1984, A new species of Temeritas (*Insecta*, *Collembola*) from China, Entotaxonomia **7**: 157-163.

DALLAI, R., V. SBORDONI, M. COBOLLI -SBORDONI, E. DE MATTHAEIS, 1983, Chromosome and enzyme diversity in some species of *Neanuridae* (*Collembola*), Pedobiologia **25**: 301-311.

DEHARVENG, L., 1980, Contribution à la connaisssance systématique, ecologique et biogéographique des Collemboles *Neanurinae* de Corse, Rev. Biol. Écol. Sol. **17**: 419-435.

DEHARVENG, L., 1981, Collemboles des iles Subantarctiques de l'Océan Indien, Mission J. Travé 1972-73. C.N.F.R.A. No. **48**: 33-108.

DEHARVENG, L., 1984, Polymorphisme et polytypisme morphologiques chez quelques *Neanurinae* européens, Rev. Ecol. Biol. Sol. **21**: 533-564.

DEHARVENG, L., 1987, Cave *Collembola* of South-East Asia, Korean Jour. Syst. Zool. **3**: 165-174.

DEHARVENG, L., B. H. LEE, 1984, Polytene Chromosomal variability of *Bilobella aurantica* (*Collembola*) from Sainte Baume population (France), Caryologica **37**: 51-67.

DELAMARE -DEBOUTTEVILLE, C., Z. MASSOUD, 1968, Révision de *Protoentomobrya walkeri* FOISOM. Collembole de Cretace, et remarquessur sa position systématique, Rev.Écol. Biol. Sol. **5**: 619-630.

DUNGER, W., 1969, Zur eignung der Apterygoten für teirgeoigraphische untersuchuchungen, Abh. Ber. Naturkundmus. Görlitz **44**: 59-64.

DUNGER, W., 1970, Zum ertorschunstand und tiergeographischen Charakter der Apterygotenfauna der Sudeten, Bulletin Entomol. de Pologne **40**: 491-496.

DUNGER, W., 1975, Collembolen aus den Börzsöny-Gebirge, Fol. Hist.-nat. Mus. Matr. **3**: 11-33.

DUNGER, W., 1985, Stand und Interesse der Ertorchung der Collembolenfauna (*Insecta*, *Apterygota*) der Mongolische Volksrepublik, Mitt. Zool. Mus. Berlin **61**: 3-10.

FANCIULLI, P. P., R. DALLAI, R. PETRUCCI, 1986, Enzymatic polymorphism in geographically isolated populations of *Thaumanura ruffoi*. (In:) R. DALLAI (ed.), 2nd International Seminar on *Apterygota*, University of Siena: 197-202.

FANCIULLI, P. P., R. DALLAI, R. PETRUCCI, 1986a, Chromosomal and isozymic anylysis in three populations of *Lathriopygia longiseta*. (In:) R. DALLAI (ed.), 2nd International Seminar on *Apterygota*, University of Siena: 203-210.

FANCIULLI, P. P., R. DALLAI, R. PETRUCCI, 1986b, A preliminary study in enzyme diversity in *Tetrodontophora bielanensis*, REBS **22**: 483-495.

FANCIULLI, P. P., F. FRATI, R. DALLAI, J. RUSEK, 1991, High genetic divergence among populations of *Tetrodontophora bielanensis* (*Insecta*, *Collembola*) in Europe, Rev. Écol. Biol. Sol. **28**: 165-173.

FJELLBERG, A., 1980, Identification keys to Norwegian *Collembola*, Norsk Entomologisk Forening Postboks **70**: 1-152.

FJELLBERG, A., 1991, *Collembola* of the Canary Islands. I. Introduction and survey of the family *Hypogastruridae*, Entomologica Scandinavica **22**: 437-456.

FRATI, F., P. P. FANCIULLI, R. DALLAI, 1992, Genetic diversity and Taxonomy in Soil dwelling Insects: the genus *Orchesella*, Jour. Heredity **83**: 275-281.

FRATI, F., P. P. FANCIULLI, L. POSTHUMA, 1992, Allozyme variation in reference and metal-exposed natural population of *Orchesella cincta*, Biochemical Systematics and Ecology **20**: 297-310.

DA GAMA, M. M., 1981, Relationship between distribution and phylogeny of *Xenylla* (*Collembola, Hypogastruridae*) species in Australia and New Zealand, Rev. Ecol. Biol. Sol. **18**: 269-284.

DA GAMA, M. M., 1986, Apercu biogeographique des Collemboles de la Macaronesie. (In:) R. DALLAI (ed.), 2nd International Seminar on *Apterygota*, University of Siena: 37-52.

DA GAMA, M. M., 1991, Collemboles (Insectes, Apterygotes) cavernicoles de la France et a Suisse, Mem. de Biospelol. **18**: 171-183.

DA GAMA, M. M., P. GREENSLADE, 1981, Relationship between the Distribution and Phylogeny of *Xenylla* (*Collembola, Hypogastruridae*) species in Australia, Rev. Écol. Biol. Sol. **18** (**2**): 269-284.

GOOD, R., 1974, The geography of Flowering Plants, Longman, London. 446 pp.

GREENSLADE, P., 1982, Origins of the collembolan fauna of arid Australia. (In:) R. BARKER & P.J. GREENSLADE (eds), Evolution of the flora and fauna of arid Australia: 267-272. Frewvale, S. Australia: Peacock Publ.

GREENSLADE, P., 1987, Zoogeography of Tasmanian *Collembola* genera. (In:) B. STRIGANOVA (ed.) 9th Colloqium on Soil Zool. Moscow 1985: 653-660.

GREENSLADE, P., 1990, Notes on the biogeography of the free-living terrestrial invertebrate fauna of Macquarie Island with an annotated checklist, Papers & Proc. Roy Soc. Tasmania **124**: 35-50.

GREENSLADE, P., L. DEHARVENG, 1991, *Phradmon*, a new genus of *Paleonurini* (*Collembola*: *Neanuridae*) from Australia with a key to the genera from southern regions and notes on *Protura*, Invertebr. Taxon. **5**: 837-854.

HANDSCHIN, E., 1926, Über Bernsteincollembolen. Ein Beitrag zur ökologischen Tiergeographie, Rev. Suisse Zool. **33**: 375-379.

HENGVELD, R., 1990, Dynamic Biogeography, Cambridge Univ. Press. 249 pp.

LESCURE, J., J. JEREMIE, W. LOURENCO, J.-P. MAURIES, J. PIERRE, C. SASTRE, J. M. THIBAUD, 1991, Biogeographie et insularite: L'example des Petites Antilles, C. R. Sceances Soc. Biogeogr. **67**: 41-59.

LINDROTH, C., H. ANDERSSON, H. BÖDVARSSON, S. H. RICHTER, 1973, Surtsey Iceland, the development of a new fauna 1963-1970, Ent. scand. Suppl. 5.

MACARTHUR, R., E. WILSON, 1967, The theory of island biogeography, Princeton University Press.

MARI-MUTT, J., 1982, Observaciones preliminares sobre la distribucion Geografica de los Collémboles de Puerto Rico (*Insecta*), Carib. Jour. Sci. **18**: 1-4.

MARI-MUTT, J., 1983, *Collembola* in amber from the Dominican Republic, Proc. Ent. Soc. Wash. **85**: 577-587.

MASSOUD, Z., 1967, Monographie des *Neanuridae*, collemboles poduromorphes a pièces buccales modifiées, Biologie de la Amérique Australe. **31**: 1-399.

MASSOUD, Z., 1967a, Contribution à l'etude de *Rhyniella praecursor* HIRST ET MAULIK 1926, Collembole fossile du Devonian, Rev. Ecol. Biol. Sol. **4**: 497-505.

MURPHY, D., 1971, Revision of the tropical marine littoral genus *Pseudanurida* SCHÖTT (*Collembola*: *Pseudachorutinae*), Pacific Insects **13**: 46-63.

NOSEK, J., 1967, The Investigation of the Apterygoten fauna of the low Tatras, Acta Universitatis Carolinae - Biologica **5/6**: 350-520.

PALACIOS-VARGAS, J., 1981, *Collembola* asociados a *Tillandsia* en el derrame lavico del Chihcinautzin, Morelos, Mexico, The S.W. Entomologist **6**: 87-98.

PALACIOS-VARGAS, J., 1988, Consideraciones biogeograficos de los microartrópodos del Popocatepetl Mexico, Folia Entomol. Mexicana **75**: 147-155.

PALACIOS-VARGAS, J., J. NAJT, 1986, *Collembola* de las reservas de la biosfera Mexicana. 1. *Neanurinae*, Folia Entomol. Mexicana **68**: 5-27.

PALACIOS-VARGAS, J., M. OJEDA, K. CHRISTIANSEN, 1986, Taxonomia y biogeografia de *Troglopedates* (*Collembola*, *Paronellidae*), Folia Entomologia Mexicana **65**: 3-35.

PARISI, V., 1969, Observations sur quelques Collemboles des iles Tavolara et Molara, Rapp. Comm int. Mer Medit. **19**: 817-819.

POINSOT, N., 1974, Documents pour une biogéographie des Collemboles de Provence, Rev. de Biologie et d'Écol. méditerranéenne **1**: 113-126.

POINSOT, N., R. DALLAI, 1971, Ricerche sui collemboli. XIII. Contributo allo studio del genere *Proctostephanus*, Redia **52**: 305-321.

RAPOPORT, E. H., 1968, Algunos problemas biogeograficos del nuevo mundo con especial referencia à la region Neotropical, (In:) DELAMARE & RAPOPORT (eds), Biologie de l'Amerique Australe, **4**: 55-104.

RAPOPORT, E. H., 1971, The geographical distribution of Neotropical and Antarctic *Collembola*, Pacific Insects Monograph **25**: 99-118.

RIEK, E., 1976, An entombryid collembolan (*Hexapoda*, *Collembola*) from the lower Permian of South Africa, Paleont. Afric. **19**: 141-143.

SCHUSTER, R., 1962, Das marine litoral als lebensraum terrestrischer kleinarthropoden, Int. Revue ges. Hydrobiologie **47** (**3**): 359-412.

SCHUSTER, R., 1964, Die Ökologie der terrestrischen Kleinfauna des Meersrtandes, Ver. Deutsche Zool. Gesell. Kiel: 492-521.

SIMBERLOFF, D., 1976, Experimental studies of Zoogeography of islands: the effect of island size, Ecology **57**: 637-648.

STOMP, N., 1986, Le groupe de *Pseudosinella vandeli* (Insectes, Collemboles) dans les Alpes Orientales. (In:) R. DALLAI (ed.), 2nd International Seminar on *Apterygota*, University of Siena: 85-91.

STRENZKE, K., 1955, XI Thalassobiont und thalassophile *Collembola*, Die Tierwelt der Nord und Ostsee **36**: 1-52.

SZEPTYCKI, A., 1967, Fauna of the springtails of the Ojców National Park in Poland, Acta Zool. Cracov. **12**: 220-274.

THIBAUD, J. M., 1990, Revision du genre *Acherontiella* ABSOLON 1913 (*Insecta*, *Collembola*), Bull. Mus. natl. Hist. nat. Paris ser. 4, **12**: 402-414.

THIBAUD, J. M., 1991, Les Collemboles des Petites Antilles V. Considerations biogéographiques et écologiques surles Collemboles Poduromorphes, Rev. Écol. Biol. Sol. **28**: 91-111.

THIBAUD, J. M., Z. MASSOUD, 1980, Etude des Collemboles de certains mileux du Maroc et considérations biogéographiques sur la faune du Maghreb, Rev. Suisse Zool. **87**: 514-548.

THIBAUD, J. M., J. NAJT, 1993, Les Collemboles (*Insecta*) de l'atoll de Fangataufa, Buli. Mus. Natl. Hist. nat. Paris 4th ser. **15**: 1-4.

TRAVE, J., 1987, Biogéographie, origine des peuplements et insularité: les microarthropodes terestres des terres australes Francaises, Actes de Colloque sur la Recherche Francaise dans les terrees australes. No. a **59**: 49-59.

VASQUES, M., J. PALACIOS-VARGAS, 1989, Une Nouvelle espece Mexicaine de *Axenyllodes* et biogeographie de la lignée *Xenyllodience* [*Collembola*, *Odontellidae*], Revue Franc. Ent. **11**: 37-41.

VUILLEUMIER, F., 1973, Insular biogeography in continental regions. II. Cave faunas from Tessin, southern Switzerland, Syst. Zool. **22**: 64-76.

WEINER, W., 1977, Zoogeographical peculiarities in the fauna of Pieniny mountains, Rev. Biol. Ecol. Sol. **14**: 39-43.

WEINER, W., 1981, *Collembola* of the Pieniny National Park in Poland, Acta Zool. Cracov. **25**: 417-500.

WITTEVEEN, J., 1986, Marine littoral *Collembola* - an ecophysiological study, Free University Press, Amsterdam. 95 pp.